Prefrontal high-gamma in ECoG tags periodicity of musical rhythms in perception and imagination

Herff, S. A.[1, 2], Herff, C.[3], Milne, A. J.[2], Johnson, G. D.[4], Krusienski, D. J.[5]

[1] *École polytechnique fédérale de Lausanne, Digital and Cognitive Musicology Lab*

[2] *Western Sydney University, MARCS Institute for Brain, Behaviour and Development*

[3] *School for Mental Health and Neuroscience, Faculty of Health, Medicine and Life Sciences, Maastricht University*

[4] *Biomedical Engineering Program, Old Dominion University*

[5] *Advanced Signal Processing in Engineering and Neuroscience Lab, Virginia Commonwealth University*

Running Head: High-gamma tags periodicity of musical rhythms

Corresponding Author:

Steffen A. Herff

E-mail: steffen.herff[at]westernsydney.edu.au

Abstract

Rhythmic auditory stimuli are known to elicit matching activity patterns in neural populations. Furthermore, recent research has established the particular importance of high-gamma brain activity in auditory processing. Here, we use electrocorticography (ECog) recordings of nine participants, to see whether high-gamma activity tracks the envelope of musical rhythms during rhythm perception and imagination. Rhythm imagination was elicited by asking the participants to imagine the rhythm to continue during pauses of several repetitions. We deploy an approach that utilizes periodicity of the signals, by computing the correlation between the autocorrelations (ACC) of both the musical rhythms and the neural signals. A condition in which participants listened to white-noise was used to establish a baseline of high-gamma activity during auditory presentation. High-gamma autocorrelations in auditory areas in the superior temporal gyrus and in frontal areas on both hemispheres significantly matched the autocorrelation of the musical rhythms. Overall, more significant electrodes are observed on the right hemisphere. Of particular interest is a large cluster of electrodes in the right prefrontal cortex that is active during both rhythm perception and imagination. This indicates conscious processing of the rhythms' structure as opposed to mere auditory phenomena. The ACC approach clearly highlights that high-gamma activity measured from cortical electrodes tracks both attended and imagined rhythms.

Keywords: ECoG, High-Gamma, Music Perception, Rhythm, Imagination, Periodicity

Neural populations match their activity patterns in response to beat and meter frequency of rhythmic auditory stimuli (Nozaradan, 2014; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Peretz, & Mouraux, 2012; Nozaradan, Zerouali, Peretz, & Mouraux, 2015). This automatic, spontaneous neural entrainment has inspired a plethora of research in music perception. For example, neural entrainment has been proposed as a mechanism through which music induces emotional affect in listeners (Trost, Labbé, & Grandjean, 2017), it is atypical in children with dyslexia, informing rhythm-based interventions (Colling, Noble, & Goswami, 2017), and neural entrainment forms the basis for neurologic music therapy in motor rehabilitation (Thaut, McIntosh, & Hoemberg, 2015). Entrainment paradigms generally require participants to tap along or listen to a rhythm instantiated by simple clicks, white noise, pure tones, or sine tones while EEG is being recorded (Nozaradan, Mouraux, et al., 2017). Using a frequency tagging approach, the continuous EEG timeseries is transformed into the frequency domain, revealing distinct enhanced frequency components at beat frequency (Nozaradan et al., 2011). However, neural entrainment to rhythmical stimuli is not exclusively driven by exogenous stimulus properties, such as an auditory stimulus, but is also shaped by endogenous top-down mechanisms, such as attention and imagination. For instance, Nozaradan et al. (2011) showed that participants listening to an isochronous stream of pure tones show differential neural entrainment depending on whether they are instructed to imagine a binary or ternary meter. This suggests that neural entrainment is not only worth investigating as a reactive process, triggered by external stimulation, but may also shed light on complex functions, such as imagination. Here, we aim to further characterise the role of neural entrainment in auditory imagination.

High-Gamma. Recent medical advances have allowed music perception research investigating neural entrainment to rhythms to venture beyond non-invasive EEG methodologies to invasive measurements such as the use of intracranial electrodes in epilepsy patients. In an intracranial study, Nozaradan, Mouraux, et al. (2017) showed that a 0-30 Hz as well as a 30-100

Hz power band track the envelope of musical rhythms. In the present study, we aim to further explore the involvement of a different power band; high-gamma.

Activity in the high-gamma band is much more localized (Miller et al., 2007) and thought to resemble ensemble spiking (Ray, Crone, Niebur, Franaszczuk, & Hsiao, 2008). Due to the small size of the generator area, frequencies above 70 Hz, become increasingly unreliable to measure, let alone localise, using EEG. In Electrocorticography (ECoG), the electrodes are deployed directly on the cortex rather than on the scalp. This enables accurate characterization of high-gamma (or Broadband Gamma, ~70-170 Hz). This is important, as high-gamma can be linked to auditory attention, auditory perception, and appears to mark auditory segment boundaries (Leuthardt et al., 2011; Pei et al., 2011; Potes, Gunduz, Brunner, & Schalk, 2012; Schalk & Leuthardt, 2011; Sturm, Blankertz, Potes, Schalk, & Curio, 2014)(see Cervenka, Nagle, & Boatman-Reich, 2011 for a review). Indeed, high-gamma acitivity can even be used to decode speech from the brain (Angrick, Herff, Johnson, et al., 2019; Angrick, Herff, Mugler, et al., 2019; Anumanchipalli, Chartier, & Chang, 2019; Herff et al., 2015; Pasley et al., 2012). When listening to music, high-gamma averaged across listeners correlates with the sound envelope of a musical piece in a data set with 7 participants (Potes et al., 2012). Using the same data set with an additional three participants, Sturm et al. (2014) found a correlation between high-gamma and the music envelope in 4 out of 10 participants. A recent study also suggests that high-gamma activity is not only involved in music listening, but also music imagination (Ding et al., 2019). In this study, participants were asked to imagination the continuation of familiar musical pieces. High-gamma activity significantly exceeded the baseline that was measured prior to stimulus onset. Using lagged correlations between high-gamma and the music's envelope, the authors investigated the time course of the activation of different brain regions.

In the present study, we aim to further investigate the potential involvement of high-gamma in music perception. However, rather than exploring familiar musical pieces, we focus

on high-gamma's involvement in musical rhythm perception as well as imagination. Here, we are also less concerned with the time-course of different brain region's activation, but rather explore areas that capture the underlying periodicities of the rhythmic signal. To do this, we deploy an adjusted frequency tagging approach.

Periodicity tagging. The current frequency tagging approaches used in music perception research focus on transforming continuous time series EEG data into the frequency domain. Typically, the power at specific frequencies of interests that are directly related to a stimulus (e.g., beat frequency) is then closer inspected (Nozaradan, Keller, Rossion, & Mouraux, 2017). The frequency areas of interest can then be compared to other non-stimulus related frequencies or to other experimental conditions. It is important to note that brain signal to stimulus approaches, and frequency tagging in particular, also come with their limitations. For example, the power of a beat-related frequency in a frequency representation of a rhythm is influenced by acoustic features of the notes that comprise the rhythm (such as note onset/offset ramp duration) (Henry, Herrmann, & Grahn, 2017). As a result, power at the beat frequency in the EEG signal becomes an unreliable measurement of entrainment. As such, neural entrainment should be understood as a relative enhancement of the beat frequency (Nozaradan, Keller, et al., 2017) in the EEG signal when listening to a rhythm compared to when not. The various acoustic features that influence the frequency representation of a rhythm also highlight the importance of taking the entire distribution of the frequency representation in both the musical as well as the brain rhythms into account, rather than considering only the beat frequencies. Furthermore, a recent discussion revolving around frequency tagging's invariance to phase information highlights the value of analyses in the time-domain (Lenc, Keller, Varlet, & Nozaradan, 2018, 2019; Novembre & Iannetti, 2018; V. G Rajendran, Harper, Garcia-Lazaro, Lesica, & Schnupp, 2017; V. G. Rajendran & Schnupp, 2019). This is because by ignoring phase information, a many-to-one matching between time and frequency domain exists. In the present study, we aim to address

some of these concerns and build on the present frequency tagging approach for repetitive acoustic rhythms by moving from a frequency representation to a periodicity tagging approach using autocorrelation representations of the data. This approach focuses on capturing and comparing similarities in the periodicity in the musical rhythm and high-gamma activity. Effectively, rather than looking for direct tracking of the envelope of musical rhythms, this approach searches for any high-gamma activity patterns that show periodicities similar to those observed in the musical rhythms. This approach retains some of the temporal information relevant to musical rhythms (e.g., in would capture example E in V. G. Rajendran & Schnupp, 2019), and represents it in a useful way to identify brain regions of interest However, the many-to-one matching is still possible. Here, we argue that if a high-gamma brain activity pattern represents or tracks the underlying periodicity of an acoustic signal, then it is most likely related to the stimulus. Indeed, there are various ways in which high-gamma activity could code the stimulus, so a many-to-one matching is not necessarily an issue when looking for areas of interest that track periodicity of stimuli. In summary, we specifically ask here, whether High-gamma oscillations during listening, as well as imagination of repetitive auditory rhythms captures the rhythms periodicities using a periodicity tagging (autocorrelation) approach.

Method

Participants. Electrocorticographic data were recorded from 8 patients (3 female, 5 male) with pharmacoresistant epilepsy undergoing localization of epileptogenic zones and eloquent cortex before surgical resection. Patients participating in this study gave written informed consent and the study protocol was approved by the institutional review boards of Old Dominion University and Mayo Clinic, Florida. Patients were implanted with subdural electrode grids or strips, based purely on their clinical need. Electrode locations were verified by co-registering

pre-operative MRI and post-operative CT. We recorded electrocorticographic activity during rhythm perception and imagination of a total of 437 subdural electrodes (see Fig.1).

Stimuli. The majority of research investigating neural entrainment use either complex speech or simple clicks, white noise, pure tones, or sine tones (Nozaradan, Mouraux, et al., 2017). To increase ecologically validity for musical stimuli, we use kick-snare drum patterns. Here, we analyse data of participants listening to two different musical rhythms. Each rhythm consists of 8 pulses and 4 sounded events. The rhythms are being presented at either 120 bpm or 140 bpm. Table 1 presents a summary of all rhythms. Rhythm 2 is a syncopated rhythm, that is listeners will perceive a downbeat on the 5th element, despite there being no sounded event. The supplemental online material S1 contains audio files of all rhythmic stimuli in both tempi. Furthermore, a control was implemented by a condition that presented white noise instead of a rhythm.

Table 1. Overview of the musical rhythms

Rhythm	**Sounded Events**	**Sequence**							
Unsyncopated	4	K	x	S	x	K	x	S	x
Syncopated	4	K	x	S	x	K	K	S	S

Note. 'K' represents a sounded Kick, 'S' represent a sounded Snare, and 'x' represent a non-sounded element.

Procedure. Each participant listened to each rhythm in blocks of 16 repetitions in 120 bpm and 20 repetitions in 140 bpm. Within each rhythm block, the rhythm dropped out for four repetitions in the 120 bpm condition and four repetitions during the 140 bpm condition and participants were instructed to imagine the rhythm to continue (imagined condition). The order of rhythm blocks was randomised. Data of additional trials that required participants to tap data along, as well as additional rhythms is reported elsewhere. ECoG signals were recorded during listening as well as imagination.

ECoG data collection. Data from the electrode grids or strips Ad-Tech Medical Instrument Corporation, Wisconsin, 1 cm spacing) were band-pass filtered between 0.5 and 500 Hz and recorded using g. USB amplifiers (g.tec, Austria) at a sampling rat of 1200 Hz. Data recording and stimulus presentation were facilitated by BCI2000 (Schalk, McFarland, Hinterberger, Birbaumer, & Wolpaw, 2004). Electrode grids for all eight participants can be seen in Figure 1.

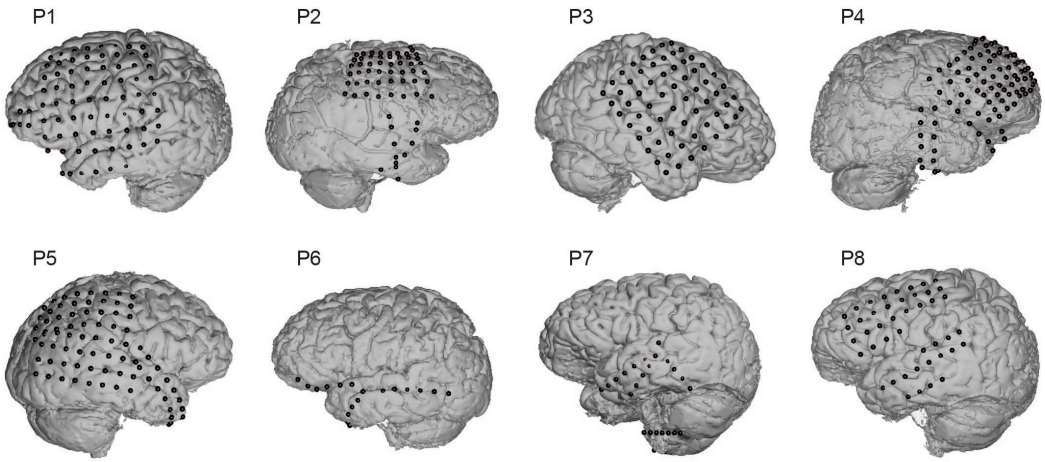

Figure 1. Electrode grid locations for all eight participants.

Data Analysis: Separately for each participant, electrode, tempo (120 bpm vs. 140 bpm), audio condition (listening vs imagine), and rhythm (Unsyncopated: K x S x K x S x vs. Syncopated: K x S K x S xx) we extracted the absolute Hilbert envelope of High-gamma activity and calculated the circular autocorrelation over all repeated presentations of the rhythm up to the Nyquist frequency. This was done by taking the real component of an inverse DFT of a pointwise multiplication of an DFT of the High-gamma timeseries and its complex conjugate and then dividing each element by the maximum element of the vector. The same transformation was conducted on the envelope of the musical rhythm's waveform. High-gamma and musical rhythm autocorrelations were correlated with one another. The resulting autocorrelation correlations

(*ACC*) between high-gamma brain activity and musical rhythms were used to statistically assess whether high-gamma tracks musical rhythms. This process is schematically represented in Figure 2. Visually, ACC can be described as the correlation between the top and bottom right panels in Figure 2. As a control, we extracted high-gamma activity, envelope and autocorrelation also for a condition where participants were listening to white noise instead of the actual musical rhythms and calculated ACC.

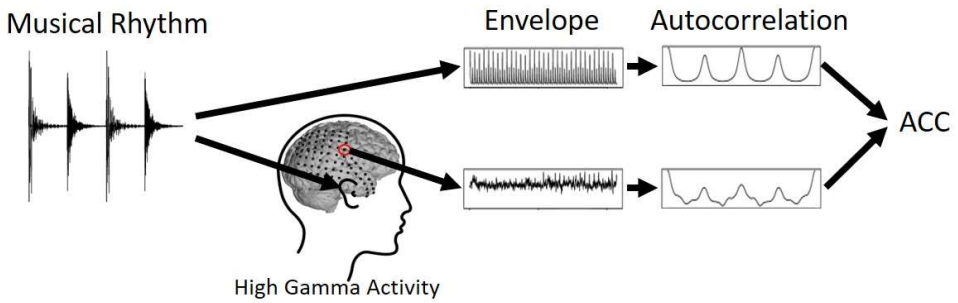

Figure 2. Schematic representation of the data analysis. The left most panel shows the original waveform of a musical rhythm. The rhythm in this example is a 'K x S x K x S x', with 'K' being the kick, 'S' the snare, and 'x' a pause. First, we extracted the envelope of the continuously looped presentation of the rhythm, as shown in the middle top panel. The top right panel then shows the autocorrelation of the rhythm's envelope. Note that the shown autocorrelation vector corresponds to the length of the original rhythm to emphasise the relationship between waveform and autocorrelation. For the actual analysis we used the whole autocorrelation vector over all repeated presentations of the rhythm up to the Nqyuist frequency. Simultaneously, we measured High-gamma activity from cortex electrodes whilst participants are listening (or imagining) the rhythm. Similar to the musical rhythm, we extracted the envelope of the high-gamma activity and calculated the autocorrelation. In a last step, we correlated the autocorrelations of high-gamma envelope and musical rhythm envelope to obtain our dependent variable: autocorrelation correlation (ACC).

We deployed a Bayesian mixed effect model predicting the correlation between the autocorrelations of high-gamma and musical rhythms (*ACC*) based on *Rhythm* (Unsyncopated. vs. Syncopated), *Tempo* (120bpm vs. 140bpm), *AudioCondition* (listen vs. imagine), and *Signal* (white noise vs. rhythm). The model was provided with a random effect for *Participant* and *Electrode*, resulting in the maximal random effect structure as justified by the experimental design (Barr, Levy, Scheepers, & Tily, 2013). The *Signal* coefficient in combination with its interaction terms allows us to inspect the evidence in favour of whether autocorrelation in high-gamma oscillation meaningfully tracks musical rhythms, whilst controlling for brain activity that a participant -at a given electrode location- would show when listening to a length-matched white noise segment instead of the actual musical rhythm. The model was provided with a weakly informative prior t(3,0,1), and ran on 4 chains with 1000 warm-ups and 10000 iterations each.

Results

For each condition, Table 2 shows coefficient estimates (β), 95%-CIs, as well as evidence ratios (Odds) for the hypothesis, that in this condition high-gamma tracks the musical rhythm. For convenience, we denote with * effects that can be considered 'significant' at an $\alpha = .05$ level (odds ratios > 19, see Milne & Herff, submitted-2019). For further details about the model and hypothesis testing, please refer to Appendix A1.

Table 2. Summary of evidence observed in each condition whether high-gamma tracks the envelope of musical rhythms.

Rhythm	Tempo	Audio Condition	β	95%-CI$_\beta$	Evidence Ratio
Unsyncopated	120	Listen	.0111	.0059 to .0164	> 9999*
Unsyncopated	120	Imagine	-.0008	-.0060 to .0044	0.66
Unsyncopated	140	Listen	.0158	.0106 to .0210	> 9999*
Unsyncopated	140	Imagine	.0108	.0056 to .0160	2768.00*
Syncopated	120	Listen	.0135	.0083 to .0187	> 9999*
Syncopated	120	Imagine	.0220	.01681 to .0272	> 9999*
Syncopated	140	Listen	.0106	.0054 to .0158	7199*
Syncopated	140	Imagine	0.0068	.0016 to .0121	61.07*

Note. In each condition, we obtain strong evidence that high-gamma oscillation tracks the envelope of musical rhythms. The only exception is the Unsycopated rhythm at 120bpm in the Imagine condition. * denote effects that can be considered 'significant' at a α= .05 level.

Strong evidence was found for all but one condition. Indeed, the Unsyncopated rhythm at 120 bpm in the imagination condition is the only case in which we do not observe strong evidence in favour of high-gamma tracking musical rhythms' periodicities. Figure 3 shows counts of the electrodes that significantly track the musical rhythms' periodicities, as well as their normalised ACC. Normalised ACC values were obtained by subtracting the significance thresholds from the observed ACCs. We calculated significance thresholds for each participant individually. For this, we used participant -and rhythm-wise the distribution of correlations between the autocorrelation of the musical rhythms and high-gamma autocorrelations whilst listening to length-matched white noise segments. Correlations that exceed 99% of this distribution are deemed significant. For the normalised ACC, this conservative significance threshold was subtracted from each ACC value.

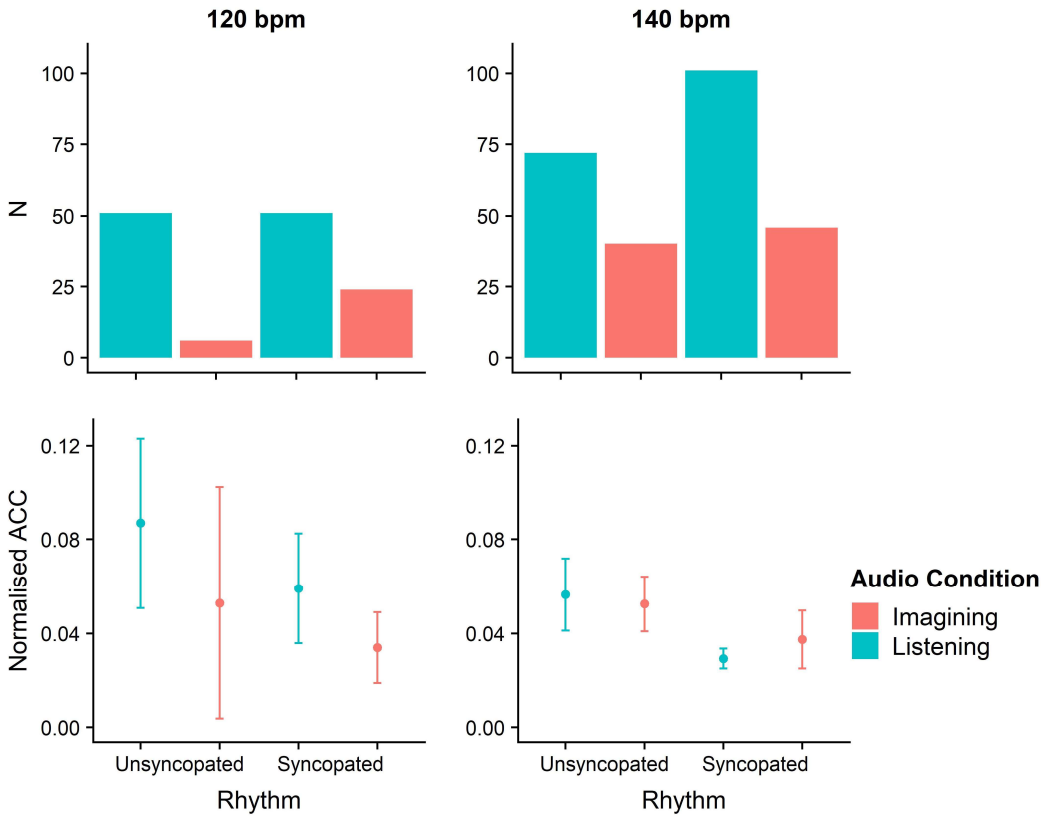

Figure 3. Number and magnitudes of electrodes that significantly track musical rhythms in their high-gamma activity. Significance was defined by exceeding participant-wise 99% of the ACC between musical rhythms and high-gamma during the white-noise control condition. Normalised ACC values were obtained by subtracting the significance thresholds from the observed ACCs. Error bars represent 95%-CIs.

Topography. To localise the effect, we plotted all electrodes on a joint brain map. Figure 4 shows electrodes with significant ACC in the audio (red), imagined (green), and both (blue) conditions.

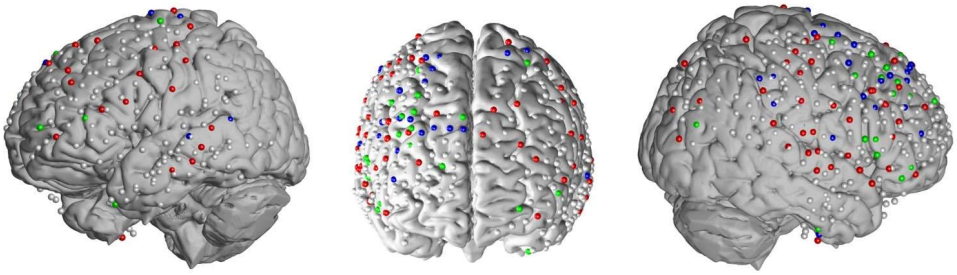

Figure 4. A joint brain map for all participants across all conditions. Electrodes in red show significant correlations between high-gamma autocorrelation and musical rhythms autocorrelations during the listening condition. Green electrode show significant ACC during the imagination condition. Blue Electrodes show significant ACC during both conditions. Significant ACCs can be observed particularly in the frontal areas of the right hemisphere. These ACCs are also significant during the imagine condition.

Discussion

The present study investigated the involvement of high-gamma in listening as well as imagining musical rhythms using brain activity of nine participants measured through invasive ECoG. Bayesian mixed effects models provided compelling support that high-gamma oscillation tracks the envelope of musical rhythms. Specifically, we deployed an analytical approach that emphasises the periodicity in musical rhythms by investigating correlations between the autocorrelations of musical rhythms' and the autocorrelation of high-gamma brain activity. In all listening conditions the models support the conclusion that high-gamma activity captures the periodicity in musical rhythms. And, we observe the same in all but one condition, when participants are imagining the rhythms, rather than listening to them. Taken together, it appears that during imagination, neural populations display the same high-gamma activity that tracks the envelope of the imagined stimulus, usually observed when acoustic stimuli are actually present. This may be preliminary support for the notion that -on a neural level- imagination involves activity of the reactive neural response associated with the presence of the stimulus.

The present finding supports previous ECoG studies that highlight the importance of high-gamma activity in auditory processing (Herff et al., 2015; Leuthardt et al., 2011; Pasley et al., 2012; Pei et al., 2011; Potes et al., 2012; Schalk & Leuthardt, 2011; Sturm et al., 2014) (see Cervenka et al., 2011). Specifically, our results replicate the findings that high-gamma tracks music envelopes (Sturm et al., 2014). Such replications are important, because ECoG studies operate with very small sample sizes. Furthermore, we extend the finding to imagination, and a periodicity tagging approach. The direct approach of directly correlating high-gamma with stimulus envelope deployed by (Sturm et al., 2014) relies on relatively long segments, clean data, and a phase-locking. The frequency tagging approach deployed by Nozaradan et al. (2011), can deal with shorter segments and more noisy data, however, is limited to key indicators in the frequency response, such as beat frequency. The periodicity tagging approach deployed here, may be a suitable compromise. Correlating the autocorrelation representations of musical and brain rhythms, and takes the whole frequency spectrum into account, whilst still emphasising the periodic nature that is essential to most musical stimuli. We found this approach useful and effective in linking brain activity to auditory stimuli, and offer it as an alternative or addition to conventional frequency tagging. Following the recent discussion about limitations of the frequency tagging approach in particular (Lenc et al., 2018, 2019; Novembre & Iannetti, 2018; V. G Rajendran et al., 2017; V. G. Rajendran & Schnupp, 2019), we consider periodicity tagging a humble compromise between frequency tagging and an analysis in the time-domain. Note, that we here correlate the two autocorrelations with one another. Other metrics of similarity such as cosine similarity, Weissman score, or shared mass might work equally well or even better. Future work could investigate the benefits of more sophisticated similarity measures.

Topography. Electrodes with significant ACCs can be found in auditory areas in the superior temporal gyrus and in frontal areas on both hemisphere. More significant electrodes are observed on the right hemisphere which is in accordance with previous findings (Thaut,

Trimarchi, & Parsons, 2014). Of particular interest is the large cluster of electrodes in the right prefrontal cortex that are active during both rhythm perception and imagined perception, which indicate conscious processing of the rhythm structure as opposed to mere auditory phenomena. This finding mirrors research that also observed frontal high-gamma when imagining familiar music (Ding et al., 2019). The previous study also found elevated high-gamma activation in the temporal lope during imagination. Here, we did not observe that high-gamma in the temporal lope represents the periodicities of the musical rhythms during imagination like the prefrontal cortex does. However, this could simply be due to a difference in methodology. The previous study (Ding et al., 2019) focused on areas that show elevated high-gamma activity and/or areas where gamma activity tracks the music's envelope. The present study uses musical rhythms rather than familiar music, and focuses on areas that track the rhythms' periodicities, regardless of overall activity. However, any area that closely tracks the audio envelope in the present dataset would have been identified by our periodicity-tagging approach, so further research is required to shed line of the role of temporal lobe during imagination.

Limitations. An important limitation in the present design is that what we and others (Ding et al., 2019) liberally term 'imagination' is in fact an 'imaginary continuation' of the rhythms. In theory, such a continuation could be functionally distinct from un-prompted imagination. In fact, it is possible that if the imagination condition would have lasted longer, then potentially the high-gamma representation of the rhythms' periodicity may have diverged. This is an empirical question for a future study. Furthermore, the one condition that did not show significant tracking of the rhythms periodicity in high-gamma urges caution interpretation of the present results. This is, because the condition was the simpler rhythm at a familiar tempo. If anything, we would have expected this condition to show the strongest effect. A possible explanation lies in the fact that this condition was always tested first. Potentially, participants were not yet familiar with the imagination task to evoke a reliable effect. Furthermore, as

common in invasive brain studies, we were operating with small participant numbers, and despite our best efforts of making the most of the data at hand, by deploying a Bayesian framework, we simply may not have the statistical power to compensate for all sources of random variability.

Conclusion

Deploying an analytical approach that emphasises the periodicity in musical rhythms, we found that high-gamma brain activity in auditory areas tracks periodicity when listening to musical rhythms. Furthermore, we found that high-gamma activity in the prefontal cortex tracks periodicity of musical rhythms both during listening and imagination.

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Author Contributions

SAH wrote the manuscript and performed the statistical analysis. CH, GDJ, and SAH pre-processed the ECoG data. AJM developed the periodicity tagging approach and SAH implemented it. DJK and GDJ designed the experiment and recorded the data. CH, AJM , GDJ, and DJK provided input on the manuscript.

References

Angrick, M., Herff, C., Johnson, G. D., Shih, J., Krusienski, D. J., & Schultz, T. (2019). Interpretation of convolutional neural networks for speech spectrogram regression from intracranial recordings. *Neurocomputing, 342*, 145-151.

Angrick, M., Herff, C., Mugler, E., Tate, M. C., Slutzky, M. W., Krusienski, D. J., & Schultz, T. (2019). Speech synthesis from ECoG using densely connected 3D convolutional neural networks. *Journal of neural engineering, 16*(3), 036019.

Anumanchipalli, G. K., Chartier, J., & Chang, E. F. (2019). Speech synthesis from neural decoding of spoken sentences. *Nature, 568*(7753), 493.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255-278. doi:10.1016/j.jml.2012.11.001

Cervenka, M. C., Nagle, S., & Boatman-Reich, D. (2011). Cortical high-gamma responses in auditory processing. *American journal of audiology, 20*(2), 171-180. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3848128/pdf/nihms533986.pdf

Colling, L. J., Noble, H. L., & Goswami, U. (2017). Neural Entrainment and Sensorimotor Synchronization to the Beat in Children with Developmental Dyslexia: An EEG Study. *Frontiers in Neuroscience, 11*, 360. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5506338/pdf/fnins-11-00360.pdf

Ding, Y., Zhang, Y., Zhou, W., Ling, Z., Huang, J., Hong, B., & Wang, X. (2019). Neural Correlates of Music Listening and Recall in the Human Brain. *Journal of Neuroscience*, 1468-1418.

Henry, M. J., Herrmann, B., & Grahn, J. A. (2017). What can we learn about beat perception by comparing brain signals and stimulus envelopes? *Plos One, 12*(2), e0172454. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5321456/pdf/pone.0172454.pdf

Herff, C., Heger, D., de Pesters, A., Telaar, D., Brunner, P., Schalk, G., & Schultz, T. (2015). Brain-to-text: decoding spoken phrases from phone representations in the brain. *Front Neurosci, 9*, 217. doi:10.3389/fnins.2015.00217

Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2018). Neural tracking of the musical beat is enhanced by low-frequency sounds. *Proceedings of the National Academy of Sciences, 115*(32), 8221-8226.

Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2019). Reply to Rajendran and Schnupp: Frequency tagging is sensitive to the temporal structure of signals. *Proceedings of the National Academy of Sciences, 116*(8), 2781-2782.

Leuthardt, E. C., Gaona, C. M., Sharma, M., Szrama, N., Roland, J., Freudenberg, Z., . . . Schalk, G. (2011). Using the electrocorticographic speech network to control a brain–computer interface in humans. *Journal of neural engineering, 8*(3), 036004.

Miller, K. J., Leuthardt, E. C., Schalk, G., Rao, R. P., Anderson, N. R., Moran, D. W., . . . Ojemann, J. G. (2007). Spectral changes in cortical surface potentials during motor movement. *Journal of Neuroscience, 27*(9), 2424-2432.

Milne, A., & Herff, S. A. (submitted-2019). The Perceptual Relevance of Balance, Evenness, andEntropy in Musical Rhythms. *Cognition*.

Novembre, G., & Iannetti, G. D. (2018). Tagging the musical beat: Neural entrainment or event-related potentials? *Proceedings of the National Academy of Sciences, 115*(47), E11002-E11003.

Nozaradan, S. (2014). Exploring how musical rhythm entrains brain activity with electroencephalogram fr equency-tagging. *Philosophical Transactions of the Royal Society B-Biological Sciences, 369*(1658). doi:UNSP 2013039310.1098/rstb.2013.0393

Nozaradan, S., Keller, P. E., Rossion, B., & Mouraux, A. (2017). EEG Frequency-Tagging and Input–Output Comparison in Rhythm Perception. *Brain Topogr*, 1-8.

Nozaradan, S., Mouraux, A., Jonas, J., Colnat-Coulbois, S., Rossion, B., & Maillard, L. (2017). Intracerebral evidence of rhythm transform in the human auditory cortex. *Brain Structure and Function, 222*(5), 2389-2404.

Nozaradan, S., Peretz, I., Missal, M., & Mouraux, A. (2011). Tagging the Neuronal Entrainment to Beat and Meter. *Journal of Neuroscience, 31*(28), 10234-10240. doi:10.1523/Jneurosci.0411-11.2011

Nozaradan, S., Peretz, I., & Mouraux, A. (2012). Selective Neuronal Entrainment to the Beat and Meter Embedded in a Musical Rhythm. *Journal of Neuroscience, 32*(49), 17572-+. doi:10.1523/Jneurosci.3203-12.2012

Nozaradan, S., Zerouali, Y., Peretz, I., & Mouraux, A. (2015). Capturing with EEG the Neural Entrainment and Coupling Underlying Sensorimotor Synchronization to the Beat. *Cerebral Cortex, 25*(3), 736-747. doi:10.1093/cercor/bht261

Pasley, B. N., David, S. V., Mesgarani, N., Flinker, A., Shamma, S. A., Crone, N. E., . . . Chang, E. F. (2012). Reconstructing speech from human auditory cortex. *PLoS Biology, 10*(1), e1001251.

Pei, X., Leuthardt, E. C., Gaona, C. M., Brunner, P., Wolpaw, J. R., & Schalk, G. (2011). Spatiotemporal dynamics of electrocorticographic high gamma activity during overt and covert word repetition. *Neuroimage, 54*(4), 2960-2972.

Potes, C., Gunduz, A., Brunner, P., & Schalk, G. (2012). Dynamics of electrocorticographic (ECoG) activity in human temporal and frontal cortical areas during music listening. *Neuroimage, 61*(4), 841-848. Retrieved from http://ac.els-cdn.com/S105381191200403X/1-s2.0-S105381191200403X-main.pdf?_tid=2874be48-74b9-11e6-aaab-00000aab0f26&acdnat=1473225107_419bf01bc142fd4d6866142507a545a8

Rajendran, V. G., Harper, N. S., Garcia-Lazaro, J. A., Lesica, N. A., & Schnupp, J. W. H. (2017). Midbrain adaptation may set the stage for the perception of musical beat. *Proceedings of the Royal Society B: Biological Sciences, 284*(1866), 20171455.

Rajendran, V. G., & Schnupp, J. W. H. (2019). Frequency tagging cannot measure neural tracking of beat or meter. *Proceedings of the National Academy of Sciences, 116*(8), 2779-2780.

Ray, S., Crone, N. E., Niebur, E., Franaszczuk, P. J., & Hsiao, S. S. (2008). Neural correlates of high-gamma oscillations (60–200 Hz) in macaque local field potentials and their potential implications in electrocorticography. *Journal of Neuroscience, 28*(45), 11526-11536.

Schalk, G., & Leuthardt, E. C. (2011). Brain-computer interfaces using electrocorticographic signals. *IEEE reviews in biomedical engineering, 4*, 140-154.

Schalk, G., McFarland, D. J., Hinterberger, T., Birbaumer, N., & Wolpaw, J. R. (2004). BCI2000: a general-purpose brain-computer interface (BCI) system. *IEEE Transactions on biomedical engineering, 51*(6), 1034-1043.

Sturm, I., Blankertz, B., Potes, C., Schalk, G., & Curio, G. (2014). ECoG high gamma activity reveals distinct cortical representations of lyrics passages, harmonic and timbre-related changes in a rock song. *Frontiers in Human Neuroscience, 8*, 798. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4195312/pdf/fnhum-08-00798.pdf

Thaut, M. H., Trimarchi, P., & Parsons, L. (2014). Human brain basis of musical rhythm perception: common and distinct neural substrates for meter, tempo, and pattern. *Brain sciences, 4*(2), 428-452.

Thaut, M. H., McIntosh, G. C., & Hoemberg, V. (2015). Neurobiological foundations of neurologic music therapy: rhythmic entrainment and the motor system. *Frontiers in Psychology, 5*, 1185.

Trost, W. J., Labbé, C., & Grandjean, D. (2017). Rhythmic entrainment as a musical affect induction mechanism. *Neuropsychologia, 96*, 96-110.

Appendix

Appendix 1A

The Bayesian Mixed effects model predicts ACC. All predictors were coded as factors. The model was provided with a weakly informative prior (t(3,0,1). The reference was placed at the Whitenoise condition, 120bpm, unsyncopated, listening condition. The model summary and 95% CIs around coefficient estimates are shown in Table A1. To assess whether high-gamma AC in the various conditions track the AC of the musical rhythms, the hypotheses tests shown in Table A2 were conducted. The results of these tests are reported in Table 2 in the main text.

Table A1. Model summary.

		AC Correlation	
Predictors	*Estimates*	*CI (50%)*	*CI (95%)*
Intercept	0.07	0.06 – 0.08	0.03 – 0.11
Rhythm	0.01	0.01 – 0.01	0.00 – 0.02
Syncopated	0.02	0.02 – 0.02	0.01 – 0.03
140bpm	-0.01	-0.01 – -0.00	-0.01 – 0.00
Imagined	0.04	0.04 – 0.05	0.04 – 0.05
Rhythm.Syncopated	0.00	-0.00 – 0.01	-0.01 – 0.01
Rhythm.140bpm	0.00	0.00 – 0.01	-0.00 – 0.01
Syncopated.140bpm	0.00	-0.00 – 0.00	-0.01 – 0.01
Rhythm.Imagined	-0.01	-0.01 – -0.01	-0.02 – -0.00
Syncopated.Imagined	0.01	0.01 – 0.01	-0.00 – 0.02
140bpm.Imagined	0.01	0.00 – 0.01	-0.00 – 0.01
Rhythm.Syncopated.140bpm	-0.01	-0.01 – -0.00	-0.02 – 0.00
Rhythm.Syncopated.Imagined	0.02	0.02 – 0.02	0.01 – 0.03
Rhythm.140bpm.Imagined	0.01	0.00 – 0.01	-0.01 – 0.02
Syncopated.140bpm.Imagined	0.03	0.02 – 0.03	0.02 – 0.04
Rhythm.Syncopated.140bpm.Imagined	-0.02	-0.03 – -0.01	-0.04 – -0.00
Random Effects			
σ^2	0.00		
τ_{00}	0.00		
ICC	0.36		
$N_{ParticipantID}$	8		
$N_{Electrode}$	584		
Observations	8352		
Marginal R^2 / Conditional R^2	0.200 / 0.558		

Table A2. Hypotheses tests behind Table 2 in the main text.

Rhythm	Tempo	Audio Condition	Hypothesis test
Unsyncopated	120	Listen	Rhythm > 0
Unsyncopated	120	Imagine	Rhythm+Rhythm:Imagined > 0
Unsyncopated	140	Listen	Rhythm+Rhythm:140bpm > 0
Unsyncopated	140	Imagine	Rhythm+ Rhythm:140bpm+Rhythm:Imagined+Rhythm:140bpm:Imagined > 0
Syncopated	120	Listen	Rhythm+Rhythm:Syncopated > 0
Syncopated	120	Imagine	Rhythm+Rhythm:Syncopated + +Rhythm:Imagined +Rhythm: Syncopated:Imagined > 0
Syncopated	140	Listen	Rhythm+Rhythm:Syncopated + Rhythm:140bpm+Rhythm:Syncopated:140bpm > 0
Syncopated	140	Imagine	Rhythm+Rhythm:Syncopated +Rhythm:140bpm+Rhythm:Syncopated:140bpm+ Rhythm:Imagined+Rhythm:Syncopated:Imagined+Rhythm:140bpm:Imagined+ Rhythm:Syncopated:140bpm: Imagined > 0